

## ROLE OF THE ANTERIOR LATERAL EYES OF THE WOLF SPIDER *LYCOSA TARENTULA* (ARANEAE, LYCOSIDAE) DURING PATH INTEGRATION

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**ABSTRACT.** Spiders of the species *Lycosa tarentula* (Linnaeus 1758) (Araneae, Lycosidae) use a vector navigation system while homing under natural conditions. Under laboratory conditions, in the absence of information relative to the sun's position or any pattern of polarized light, *L. tarentula* uses a path integration system which consists of turning at a fixed angle similar to one that could carry it to its burrow. In the absence of light, the angle is random. In this study we ask whether the spiders acquire the information about the angle turned during the outward journey through the anterior lateral eyes (ALEs), whose visual fields are directed towards the ground. To answer this question, two groups of animals were studied: one group with only the ALEs covered and another group with all eyes except ALEs covered. Our results show that ALE information alone is adequate to obtain the angle at which the animal should turn when homing.

**Keywords:** Direction estimation, spiders, optical flow

Animals that are central foragers move from a central point (nest, burrow) to find food or mates. After this displacement, these animals must be able to reach that central point. Path integration (PI) is one of the most frequently used mechanisms to get it (Papi 1992). While moving, the animal measures and integrates the angles (rotations) as well as distances travelled to obtain a vector whose orientation indicates home direction and whose length indicates the distance, so that it can always take a direct path back to its starting point. That means that the animal does not retrace its outward journey.

Information about changes of direction can be obtained in arthropods through exoskeletal sense organs (Seyfarth et al. 1982; Mittelstaedt 1983; Görner & Claas 1985; Durier & Rivault 1999) or by the use of biological compasses based on the sun or the pattern of celestial polarized light (Wehner 1997; Homberg 2004; Mappes & Homberg 2004). In several insects, it has been shown that they use translational image motion (optic flow) to estimate flight- or running distances (review: Srinivasan & Zhang 2004). In particular, several studies made with honeybees (Srinivasan et al. 1997) demonstrated that honeybees integrate over time the image velocity that is experi-

enced during the flight and that this measurement is independent of image structure (Si et al. 2003). In another experiment, Ugolini (1987) displaced wasps from their nests to various sites, released them, and observed their homing trajectories. He found that they headed accurately towards their nests if they had been displaced in a transparent container but not when they had been displaced in an opaque container.

In spiders, homing has been thoroughly studied in the funnel web spider *Agelena labyrinthica* (Clerck 1757), which can use visual cues together with tactile and proprioceptive ones (Görner & Claas 1985). Homing has also been studied in the nocturnal ctenid spider *Cupiennius salei* (Keyserling 1877) (Seyfarth & Barth 1972; Seyfarth et al. 1982; Barth 2002). It was demonstrated that *C. salei* needs proprioceptive information for homing because animals that have been surgically altered (e.g., spiders with the lyriform slit sense organs of the femur and tibia destroyed mechanically) returned with less success to the site from which they had been chased. In *C. salei*, Schmid (1997) noted differences in the kind of locomotion depending upon whether they were in bright light (normal walking movements with eight legs) or complete darkness (first pair of legs used as antennae).

In Lycosidae, the first studies about homing were realized in the European species *Arctosa perita* (Latreille 1799) (Papi 1955; Papi & Tongiorgi 1963). This species displays so-called "zonal orientation" or "orientation to Y axis," which means that after an active or passive displacement away from the shore, they orient and move perpendicular to the shore until they reach it. Papi (1955) demonstrated that *A. perita* could find the shore from which it had been displaced only if the sky was not heavily overcast. Later, the contributions of innate and learned components to astronomical orientation were analyzed by Papi & Tongiorgi (1963). Magni et al. (1964) showed that the anterior median eyes (AMEs) were primarily responsible for homing behavior by using celestial polarized light in *A. variana* Koch 1847. However, the structural basis for polarization sensitivity in AMEs was not found (Bacetti & Bedini 1964). The first study that discovered the structural basis for polarization sensitivity in Lycosidae was by Melamed & Trujillo-Cenoz (1966) in *Lycosa erythrognatha* Lucas 1836 (= *L. raptoria* Walckenaer 1837) followed by the research on *L. tarentula* (Linnaeus 1758) (Kovoor et al. 1993). Recently, Dacke et al. (2001) have found the same structural basis in *Lycosa godffroyi* L. Koch 1865 and other lycosids.

*Lycosa tarentula* is a circum-Mediterranean wolf spider that typically lives in a burrow in which the superior part is delimited by little twigs held together by silk (Ortega-Escobar 1986). The depth and diameter of the burrow is correlated with the spider's size (Ortega-Escobar 1986). The prosoma of *L. tarentula* females is variable in size: it can measure from 6.0–9.5 mm in width (unpub. data).

The visual system of the lycosid spider *Lycosa tarentula* has been studied both from the behavioral (orientation to nest: Ortega-Escobar & Muñoz-Cuevas 1999; Ortega-Escobar 2002a; locomotor activity rhythms: Ortega-Escobar 2002b; Ortega-Escobar et al. 1992) and structural aspects (Kovoor et al. 1992, 1993, 1999, 2005a, b). In the study by Ortega-Escobar & Muñoz-Cuevas (1999), when spiders were under an overcast sky, they did not orient homewards; instead, they turned an almost constant angle for PI or path integration. In an indoor study (Ortega-Escobar 2002a), individuals of *L. tarentula* were displaced by moving them along a two-leg trajectory with

a 90° angle between legs; at the end of the outbound path, the spider was lifted and placed in an arena with its body axis oriented at random. When this procedure was carried out under illumination, the spiders showed PI by turning a constant angle and walking in search of the burrow, while in darkness (really under red light to which they are insensitive) they also showed PI but in this case they turned a random angle. Thus, it is possible that *L. tarentula* needs visual information about their movement (optic flow) and given the visual fields of their eyes (Land 1985), the eyes that could give more precise information about optic flow would be the anterior lateral eyes (ALEs) which look towards the ground. The aim of the present study was to check what eyes provide to *L. tarentula* the most reliable information about directional changes in PI in the laboratory in the absence of celestial cues. In a first approach, I have analyzed the contributions of anterior lateral eyes (ALEs) versus the rest of the eyes.

## METHODS

**Experimental animals.**—Twelve lab-reared adult females of *L. tarentula* were used. They were maintained in individual containers measuring 17 × 13 × 8 cm, big enough for them to move around to dig burrows. They were fed blow flies (*Calliphora vomitoria*) and given water twice a week. These animals had been captured from a wild population in Madrid (central Spain; N 40° 32' W 3° 42') and went through the final 2–3 molts in the laboratory; all were close to the same age and all trials were conducted after maturation.

**Experimental procedure.**—To begin the study of homing orientation, animals were placed in a terrarium measuring 60 × 30 × 35 cm. This terrarium had a 15 cm deep substratum of soil similar to the natural substrate (Fig. 1 right); in the middle of one long side of the terrarium, an artificial burrow was built, similar to that which the spider digs in the field. After 5 days of habituation to the terrarium, the experiment began. During these 5 days, spiders were mostly in the burrow during the daytime and moved about during some hours at night. To displace the spiders, they were gently removed from the burrow and pushed along the edge of the terrarium on a path traversing half the length and the full width of the terrarium. When the spider ar-

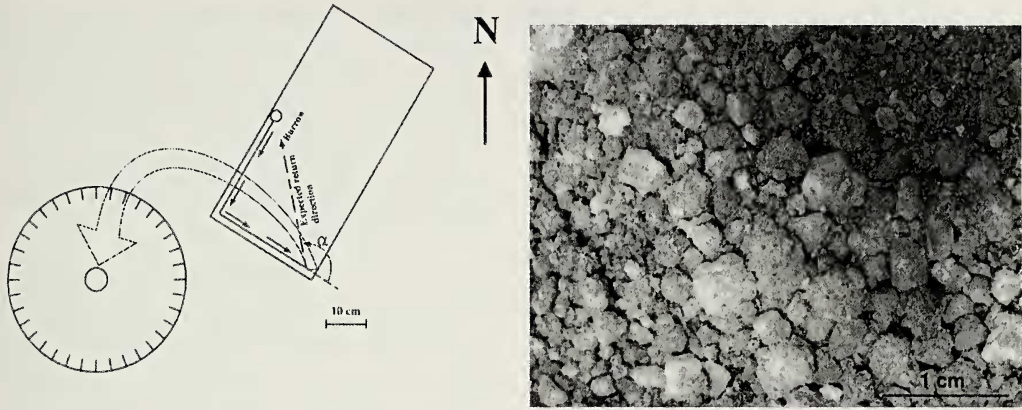


Figure 1.—*Left*: Setup used to study homing in *L. tarentula*. *Right*, top view of terrarium in which the animal lived during the study; arrows indicate the outward path. *Left*, dorsal view of the arena in which the animal was left after being taken from the right corner opposite to the burrow. Burrow direction was at  $350^\circ$ . The big arrow indicates the transfer of the animal to the center of the arena (shown at half of its actual size in relation to the terrarium). To go to the burrow, the spider must turn an angle of  $135^\circ$  in its terrarium. *Right*: Aspect of the substratum of the terrarium.

rived at the end of the path, it was placed into a transparent open glass container and transferred to the center of an arena 90 cm in diameter (wall height, 48 cm; visual angle,  $47^\circ$ ) (Fig. 1 left). There, if the animal turned at an angle of  $135^\circ$  towards the left, it would be oriented to its burrow. Both the terrarium and the arena were in a room without natural lighting. The room was lit in the daytime (0800–2000 h) with white light by two SYLVANIA<sup>®</sup> Standard F36W fluorescent tubes producing 200 lux at the floor level of the arena. Each animal was used in 8 trials (eight control trials and eight experimental trials; see below) and placed in one of the following compass directions at random:  $0^\circ$ ,  $45^\circ$ ,  $90^\circ$ ,  $135^\circ$ ,  $180^\circ$ ,  $225^\circ$ ,  $270^\circ$ ,  $315^\circ$ . The spider's orientation was recorded when it was at a distance of 20 cm from the center of the arena. If the spider had not moved during 20 minutes it was returned to the terrarium. The floor of the arena was thoroughly cleaned with ethanol before each test. All the trials were run between 11 and 18 h with lights on.

All spiders ( $n = 12$ ) were observed first with all eyes uncovered (control test; eight trials for each animal). Afterwards, spiders were assigned at random to one of two groups. One set of spiders ( $n = 6$ ) had all eyes but the ALEs covered (uncovered ALEs group, experimental test), while the other set ( $n = 6$ ) had only the ALEs covered (covered ALEs group, experimental test). Therefore, we had

two groups: “uncovered ALEs group” and “covered ALEs group” that were observed without eye covering (control test) and with eye covering (experimental test). To cover the eyes, the animals were anesthetized with ether, their legs restrained with adhesive plaster and their eyes covered by first applying a layer of collodion over the anterior region of the prosoma; then by applying two layers of water-soluble black paint (Van Gogh); and, finally, by applying another layer of collodion. Eye occlusion was checked in each case after the completion of runs using a stereo microscope.

**Automated video tracking.**—The image of the arena was captured by an Ikegami ICD-42B B/W CCD video camera and displayed on a Sony<sup>®</sup> Trinitron color video monitor. Simultaneously, the video signal was digitized by a Targa 1 frame grabber that was interfaced with a personal computer supporting an object video-tracking system (Etho-Vision, Noldus Information Technology, Wageningen, The Netherlands). The paths supplied by Etho-Vision were later digitized. The best-fitting line to a trajectory was computed by the method of principal axes (Sokal & Rolf 1995).

The following parameters were determined in both conditions (covered or experimental and uncovered or control eyes) in both groups: (1) topographic bearing of the digitized homeward path when the spider crossed a virtual circle 20 cm in diameter from the starting point of the return; (2) angle ( $\alpha$  angle) of the

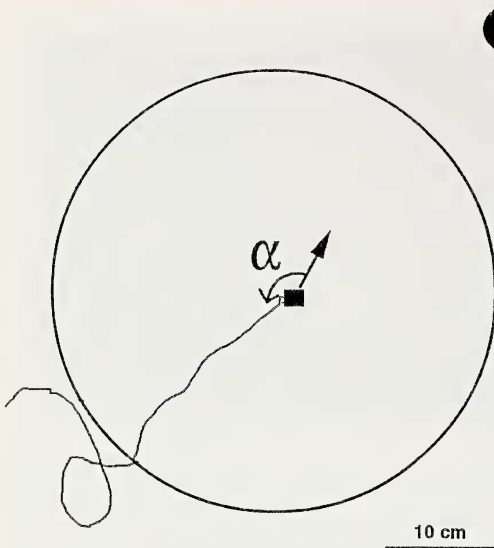


Figure 2.—Example of a homeward path in the arena. The black square in the center represents the point where the spider is placed, and its orientation is indicated by the arrow; the black circle represents the burrow compass direction;  $\alpha$  is the angle between the initial orientation and final bearing (where homing path crosses the circle).

body axis when the spider crossed the virtual circle with respect to the starting position of the body axis; as the animal could turn either clockwise or counterclockwise, the  $\alpha$  angle was always taken counterclockwise, which was the expected direction for the animal to turn in the terrarium (Fig. 2); (3) turning direction (clockwise or counterclockwise).

**Statistical analyses.**—The directions followed by the animals were analyzed as circular variables according to Batschelet (1981). For first-order statistics, the Rayleigh test was used to determine whether the observed homing directions from particular individuals were significantly oriented. To see if the deviation between individual significant vectors and the angle of home direction (Fig. 2) was significant we used the confidence interval for the mean angle ( $P < 0.05$ ; Batschelet 1981). On the second-order level, Moore's and Mardia-Watson-Wheeler's tests (Batschelet 1981) were used to test directionality significance and differences in the orientation of the subjects between control and experimental tests respectively.

The percentage of turning in the correct direction (counterclockwise) was analyzed by a

two X two repeated measure analysis of variance with the type of eyes (PMEs/PLEs/AMEs, and ALEs) and covering (control - without eye covering-, and experimental -with eye covering-) as factors.

Voucher specimens have been deposited in the Museo Nacional de Ciencias Naturales (Madrid, Spain).

## RESULTS

**Homing in uncovered ALEs group (control test).**—Homing paths followed by the spiders in the arena were either roughly straight, finishing with a sudden turn either to the right or to the left, followed by a turn in the opposite direction, as described previously (Ortega-Escobar 2002a) or they walked until they touched the arena wall. This series of turns has also been observed when the animal is taken from the burrow without having been displaced and transferred to the center of the arena. This type of behavior, called "systematic search" (Wehner & Wehner 1986), was not analyzed in this study.

**Topographic bearings:** None of the six spiders oriented themselves towards the burrow position or towards another point of the room in a constant way in the eight trials (Fig. 3 top, left).

**$\alpha$  angle:**  $\alpha$  was non-randomly oriented in all six animals (Table 1 and Fig. 4 top, left). The mean vectors of the six animals were not randomly distributed (Moore's test:  $D = 1.277$ ,  $P < 0.05$ ). Table 1 shows the mean angle and length of the vector for each animal. In two animals the turn that the spider should have made to go to the burrow in the terrarium ( $135^\circ$ ) was included in the confidence interval of the mean, but their mean vectors were statistically significant (Fig. 4 top, left).

**Homing in uncovered ALEs group (experimental test).**—The homing paths in the experimental test were similar to those shown by animals when all eyes were uncovered.

**Topographic bearings:** Only one of the six spiders oriented itself towards one point of the room in a consistent way in the eight trials. (Fig. 3 bottom, left). The other five animals oriented themselves at random.

**$\alpha$  angle:**  $\alpha$  was non-randomly oriented in all six animals (Table 1 and Fig. 4 bottom, left). The mean vectors of the six animals were not randomly distributed (Moore's test:  $D = 1.353$ ,  $P < 0.05$ ). Table 1 shows the

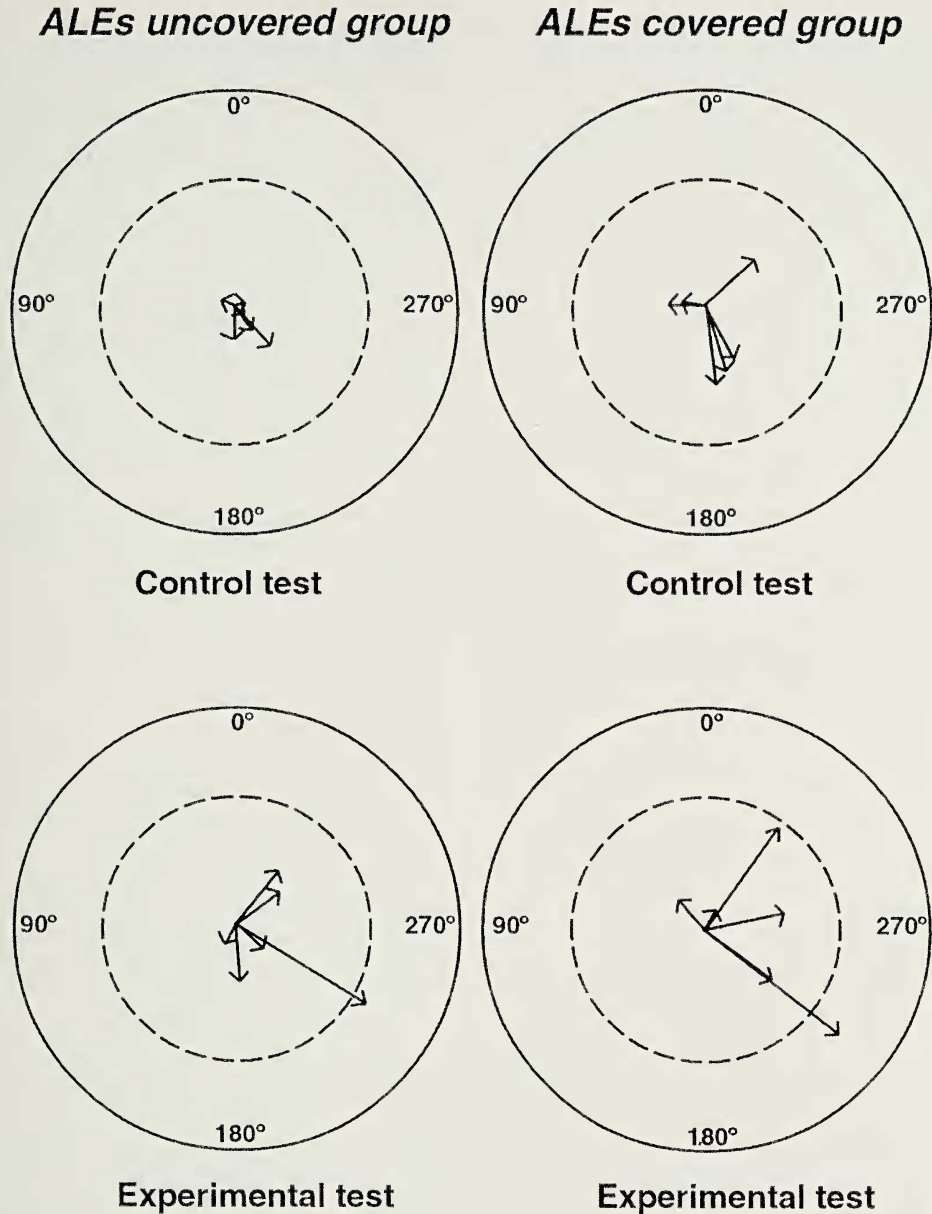


Figure 3.—*Top left:* Mean vectors (control test) of topographical bearings of the uncovered ALEs group. The dashed circle indicates the critical  $r$ -value of  $P = 0.05$ .  $0^\circ$  indicates the magnetic North. *Top right:* Mean vectors (control test) of topographical bearings of the covered ALEs group. *Bottom left:* Mean vectors (experimental test) of topographical bearings of the uncovered ALEs group. *Bottom right:* Mean vectors (experimental test) of topographic bearings of the covered ALEs group.

mean angle and length of the vector for each animal. In four animals, the turn that the spider had to make to go to the burrow in the terrarium ( $135^\circ$ ) was included in the confidence interval of the mean.

**Homing in covered ALEs group (control test).**—As expected, the homeward paths of

these animals were very similar to those observed for the other group (ALEs uncovered group).

*Topographic bearings:* None of the six spiders oriented itself towards the burrow position or towards another point of the room in a consistent way in the eight trials (Fig. 3 top, right).

Table 1.— $\alpha$  angle (mean  $\alpha$  angle ( $\theta$ ) and vector length ( $r$ )) in the controls and tests of both groups. Asterisks indicate the degree of significance of the first and second order data; \*,  $P < 0.05$ .

Individual	Covered ALEs group				Individual	Uncovered ALEs group			
	All eyes uncovered		ALEs covered			All eyes uncovered		ALEs uncovered	
	$\theta$	$r$	$\theta$	$r$		$\theta$	$r$	$\theta$	$r$
1	159°	0.87*	61°	0.39	1	154°	0.81*	146°	0.80*
2	38	0.71*	42	0.56	2	164	0.83*	172	0.80*
3	134	0.65*	318	0.14	3	169	0.74*	158	0.91*
4	165	0.66*	51	0.27	4	165	0.95*	154	0.93*
5	161	0.87*	204	0.69*	5	195	0.91*	187	0.75*
6	60	0.68*	55	0.55	6	122	0.94*	137	0.96*
Group means	126	0.64	42	0.51		162	0.93*	159	0.96*
Mardia test	$R_1^2 = 14.91, P < 0.05$				$R_1^2 = 0.27, NS$				

$\alpha$  angle: The  $\alpha$  angle (Fig. 4 top, right) was non-randomly oriented in all the animals of this group. The mean vectors of the six animals were randomly distributed (Moore's test:  $D = 0.923, P > 0.05$ ). Table 1 shows the mean angle and length of the vector for each animal. In four animals the turn that the spider had to make to go to the burrow in the terrarium ( $135^\circ$ ) was included in the confidence interval of the mean. In the other two animals, the  $135^\circ$  value was not included in the confidence interval of the mean, but their mean vectors were statistically significant (Fig. 4 top, right).

**Homing in covered ALEs group (experimental test).**—The homeward paths of the animals with covered ALEs were very similar to those observed when no eye was covered. However, in several animals, circular pathways were observed (Fig. 5). These circular pathways were not used for the analysis.

**Topographic bearings:** Only one of the six spiders oriented itself towards a point of the room in a consistent way in the eight trials (Fig. 3 bottom, right).

$\alpha$  angle: The  $\alpha$  angle (Fig. 4 bottom, right) was randomly oriented in all but one of the animals of this group. In this animal, this angle (Table 1) has a value of  $204^\circ$ , very different from  $135^\circ$ ; this value was not included in its confidence interval.

**Comparison of  $\alpha$  angle in control tests between both groups.**—To test if both groups have the same mean orientation in control tests we have used the Mardia-Watson-Wheeler test. In this case,  $R_1^2 = 1, NS$ , therefore there is no difference in the  $\alpha$  angle between both groups.

**Percentage of turning in the expected direction (see Methods).**—Turning in the expected direction by the six animals of the uncovered ALEs group (control test) was  $70.8 \pm 6.5\%$  (mean  $\pm$  SD), while among the six in the covered ALEs group (control test) it was  $87.5 \pm 19.4\%$  (Fig. 6).

In experimental tests,  $75 \pm 22.4\%$  of the animals with only the ALEs uncovered turned in the expected direction while  $50 \pm 22.4\%$  of those animals with only ALEs covered turned in the expected direction.

The ANOVA of the percentage of turning in the expected direction showed no effects for the two factors and significant effects for the interaction ( $F_{1,10} = 15.625, P = 0.003$ ).

## DISCUSSION

As in a previous study (Ortega-Escobar 2002a), the present results show that during the day *L. tarentula* does not orient itself towards the topographic burrow position in the absence of tacto-chemical information and the presence of distant visual landmarks of the laboratory. The results agree with what has been observed when the animals could use neither the sun nor the polarized light pattern for homing (Ortega-Escobar & Muñoz-Cuevas 1999).

With all the eyes uncovered, this study shows that *L. tarentula* tries to return home by turning a fixed angle,  $\alpha$ , near to  $135^\circ$ . The turn near to  $135^\circ$  would let the animal walk to a point near the burrow if its orientation had not been changed in the arena.

If *L. tarentula* used only proprioceptive information for homing, it should be able to turn an  $\alpha$  angle near to  $135^\circ$  when it was displaced

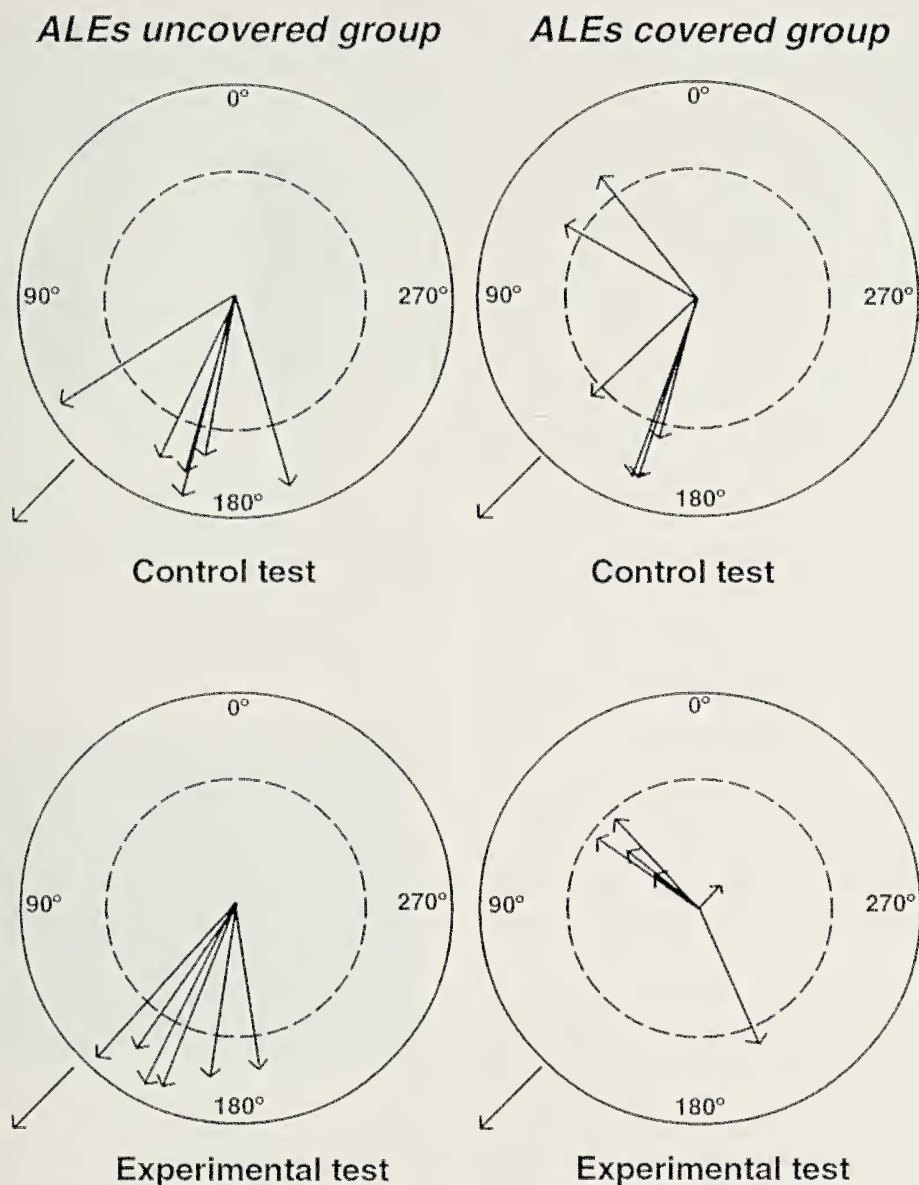


Figure 4.—*Top left:* Mean vectors (control test) of  $\alpha$  of the uncovered ALEs group. The dashed circle indicates the critical  $r$ -value of  $P = 0.05$ .  $0^\circ$  indicates that the animal walks in the same direction that it has been placed in the arena. The external arrow represents the angle the spider has to turn in the terrarium to go back to the burrow ( $\alpha = 135^\circ$ ). *Top right:* Mean vectors (control test) of  $\alpha$  of the covered ALEs group. *Bottom left:* Mean vectors (experimental test) of  $\alpha$  of the uncovered ALEs group. *Bottom right:* Mean vectors (experimental test) of  $\alpha$  of the covered ALEs group.

in the darkness. The previous study (Ortega-Escobar 2002a) had shown that this is not the case. Therefore, there must be some kind of visual information that the spider must use for homing. The present results exclude the possibility of using distant visual landmarks given that topographic bearings are not constant.

There is another possibility to estimate the angle  $\alpha$ : the use of the self-induced optic flow through some eyes. The visual field of ALEs is disposed in such a way that optic flow through them is more constant than optic flow through the other eyes (Fig. 7). As the animal walks, the distance to the ground is rather con-

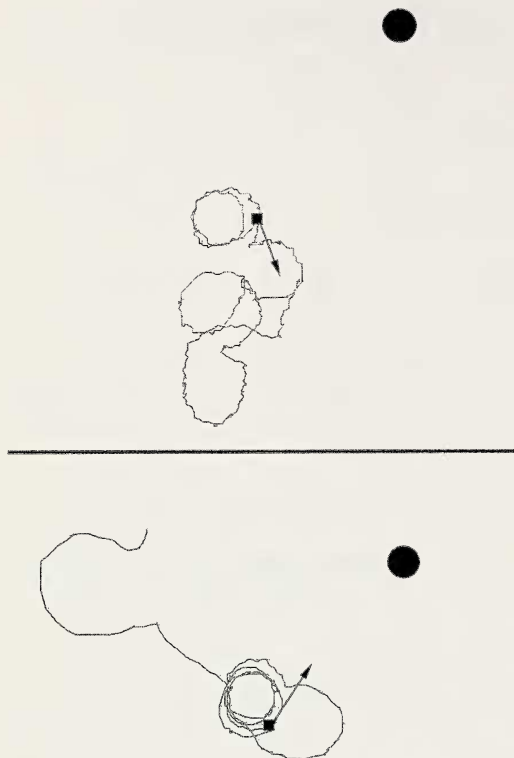


Figure 5.—Two examples of homeward paths of two different spiders with only ALEs covered. Black square represents the initial position of the spider; arrow represents the initial body direction; black circle represents burrow direction.

stant and they mainly image the ground on which the animal walks. On the other hand, the other eyes image different objects and the optic flow is more complex in relation to the distance to the eyes. It is proposed that *L. tarentula* is able to perceive the optic flow of the natural soil of the terrarium where it is displaced, and afterwards it uses this information to turn in the correct direction and angle even if it is placed over an unstructured substrate such as the white substratum of the arena. Are the ALEs able to discriminate the small pebbles of the terrarium soil? One measure of the resolution capacity of a simple eye is the sampling frequency,  $\nu_s$  (Land & Nilsson 2002) such that  $\nu_s = 1 / (2\Delta\Phi)$  where  $\Delta\Phi$  is the inter-receptor angle. Using the values obtained by Kovoor & Muñoz-Cuevas (1996/1997) for *L. tarentula* female, for the ALEs  $\nu_s = 0.30$  cycles/degree which means that a grating consisting of two stripes, one black and one white, will occupy  $3.33^\circ$  of the visual field.

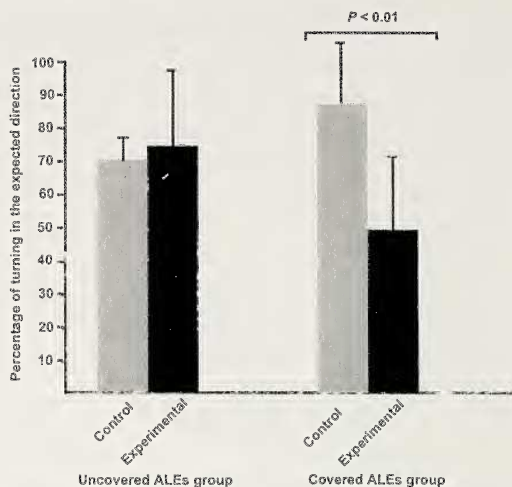


Figure 6.—Percentage of turning in the expected direction (mean  $\pm$  SD) in the control and experimental tests of both groups.

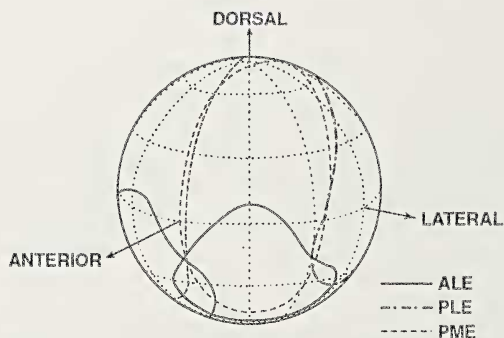


Figure 7.—Top: Frontolateral picture of *L. tarentula* showing the positions of the eyes. ALE: Anterior lateral eye; AME: Anterior median eye; PLE: Posterior lateral eye; PME: Posterior median eye. Bottom: Schema showing the visual fields of the different eyes of *Lycosa tarentula* (taken from Land 1985).



Supposing that the distance between the ALEs and the soil is 1 cm, the sampling frequency of these eyes is high enough to distinguish between the small pebbles that the spider finds while she walks about in the terrarium. Additional experiments will be needed in which the animal is trained to walk in an artificial structured environment (e.g., a grating of black and white stripes with a certain frequency) and then tested in an unstructured environment (white substratum) or a differently structured one (e.g., a grating perpendicular to the training one).

The main results presented in this study (Figs. 4 & 6) clearly demonstrate that visual input gathered through ALEs influences the spider's estimate of the turning angle to reach home. The mean vectors of animals with only ALEs uncovered do not differ statistically from the mean vectors of these animals when they could use visual information gathered through all eyes.

However, the results obtained when all the other eyes (PMEs, PLEs, and AMEs) were uncovered and only ALEs covered show that the visual information gathered through the former eyes is not usable for homing. In fact, results under this condition are not different from those obtained when animals walked in darkness during the outward and homeward paths (Ortega-Escobar 2002a). Anterior lateral eyes seem to transfer information about the direction of turning and the angle turned because when they are not functional, the animal turns clockwise or counterclockwise at random and at a random angle.

In the wild in the daytime, female *L. tarantula* walk out of their burrows only when there is prey or another member of the species present, while at night they walk out spontaneously. This behavior must also be based on some differences between the states of the eyes in the day and at night and between the visual fields of the different eyes. *Lycosa tarantula* would achieve PI by using proprioceptive and visual information gathered through the anterior lateral eyes (ALEs), which have ventral visual fields whose images change very little when the animal walks in comparison with the images through the anterior median (AMEs), posterior median (PMEs) or posterior lateral eyes (PLEs), which move quickly, given their visual fields. This is the easiest way to associate the proprioceptive

with the visual information generated by the ALEs. Besides, the rhabdoms of the ALEs have been shown (Kovoor et al. 1995) to be capable of functioning well between 12 and 19 h, the time when these experiments were carried out. In the PMEs and PLEs, membrane synthesis takes place at this time, and they are not in a good functional state. However, they probably could function well under a light intensity higher than that used in this experiment.

It seems that there is a specialization in the functioning of *L. tarantula* eyes as it has been proposed for another lycosid, *Rabidosa rabida* (Walckenaer 1837) (Rovner 1993) and for the ctenid *Cupiennius salei* (Schmid 1998). ALEs are specialized for navigation when sun/polarized-light pattern compasses are not available and to set the locomotor activity rhythm to LD cycles (Ortega-Escobar 2002a, b). AMEs are specialized for navigation with the sun or the pattern of polarized light (Ortega-Escobar & Muñoz-Cuevas 1999). PMEs do not seem to function in homing (this study; Ortega-Escobar & Muñoz-Cuevas 1999) but other studies (Rovner 1993) suggest that they are involved in recognizing form.

In the other two well-studied spiders, *Cupiennius salei* and *Agelena labyrinthica*, the possible differential role of the eyes in path integration has not been studied in the former, but it has been well documented in the latter (Görner & Claas 1985). *Cupiennius* (Seyfarth et al. 1982) was studied in a situation in which it could be shown that the spider did not need to retrace its outward journey; but animals with specific eye coverings were not studied. In *A. labyrinthica*, "the experiments to date have not revealed whether the different types of eye have separate functions with respect to optical navigation by a light source" (Görner & Claas 1985: p. 281). Consequently, the kind of visual navigation studied in *A. labyrinthica* was quite different from the present study of *L. tarantula*, and no comparison is possible.

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